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# Coccolithophorids in Polar Waters: *Calciarcus* spp. Revisited

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**Abstract.** The genus *Calciarcus* is revisited here with the purpose of providing, based on additional sampling from both polar regions, an update on species diversity and morphology that can serve as a reference for future work. The geographic realm of the genus is significantly widened and a case is built based on consistency in appearance in favour of adding *Calciarcus* spp. to the well-defined community of bipolar weakly calcified coccolithophorid genera. Despite the multitude of specimens available for analysis and the fact that the specimens examined distribute themselves within three clusters based on morphological features of coccolith superstructures, it has not been possible at this stage to define a robust framework for differentiation among species of *Calciarcus.* Circumstantial evidence exist linking species of *Wigwamma* with species of *Calciarcus* in haploid-diploid life cycles.

**Key words:** Coccolithophorid, holococcolith, *Calciarcus*, polar regions, electron microscopy.

**Abbreviations:** TEM – transmission electron microscope; SEM – scanning electron microscope; LM – light microscope; AMERIEZ, EPOS, ANT X/3, NBP – acronyms for Antarctic cruises (see Materials and Methods); NEW, NOW – acronyms for Arctic cruises (see Materials and Methods).

## INTRODUCTION

A range of weakly calcified coccolithophorids (Haptophyta) were found to be consistently present at high latitude sampling sites during investigations undertaken almost four decades ago (Manton and Oates 1975; Manton and Sutherland 1975; Manton *et al.* 1976a,b, 1977; Thomsen 1980a,b,c,d, 1981; Thomsen *et al.* 1988, 1991). The material utilized was in all cases natural water samples processed directly for transmission electron microscopy. The overarching thematic focus of these early publications was an ultrastructural mapping of external cell coverings in support of establishing a taxonomic framework for the suite of new polar taxa. Subsequent attempts to establish any of these taxa in culture, which would render possible the application of e.g. molecular biological tools or advanced electron microscopical thin sectioning techniques, have so far been unsuccessful. This means that our knowledge of these organisms, e.g. with regard to their phylogenetic position within the haptophyte realm is still scanty. However, features such as the ability to conquer severe environmental constraints of life at high latitudes (e.g. a low temperature and low light regime) and a life strategy

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which in contrast to other coccolithophorids does not involve photosynthesis (Marchant and Thomsen 1994) clearly identify these polar organisms as a potentially very interesting research subject of major relevance to coccolithophorid research at large.

A literature search covering the interim period since the introductory description of the weakly calcified polar coccolithophorid taxa reveals very few hits on any member of this contingent of species thus adding little to their known biogeographical ranges. However, a recent paper by Charalampopoulou *et al.* (2011) confirms, based on material from e.g. Svalbard, the existence and uniqueness of this high latitude community of weakly calcified coccolithophorids (*Wigwamma*, *Pappomonas*, *Papposphaera*). They report cell abundances of < 3 cells $ml^{-1}$ and conclude based on a multivariate approach, that high pH values and low temperatures are the most significant environmental variables contributing to a clear cut separation of the Svalbard community from other assemblages studied along a transect from the southern part of the North Sea to the marginal ice edge north of Svalbard.

This paper is the second in a series of publications that in turn revisits all the weakly calcified coccolithophorid genera and species based on a series of Arctic and Antarctic field sampling campaigns. While the first paper (Thomsen *et al.* 2013) elaborated on species of *Wigwamma* Manton *et al.* 1977 and further introduced a new genus, viz. *Pseudowigwamma* Thomsen in Thomsen *et al.* (2013), to accommodate *Wigwamma scenozonion* Thomsen 1980c, this paper revisits the holococcolithophorid genus *Calciarcus* Manton *et al.* 1977. Circumstantial evidence exist (Thomsen *et al.* 1991, Thomsen *et al.* 2013) in favour of nominating the holococcolithophorid genus *Calciarcus* as a life cycle counterpart of the heterococcolithophorid genus *Wigwamma*. It is now a generally accepted fact (see e.g. Billard 1994; Cros *et al.* 2000; Houdan *et al.* 2004, 2006) that the vast majority of extant coccolithophorids form part of a haploid-diploid life cycle, where both the diploid heterococcolithophorid stage and the haploid holococcolithophorid stage can multiply asexually for extended periods of time. The rare findings of combination cells that encompass both hetero- and holococcoliths in the very same periplast provide evidence in favour of establishing such life history dependencies of taxa that were previously treated as separate entities. The actual triggers behind a phase-change are at present insufficiently accounted for, although chances are that nutrient scarcity, light conditions and genetic plasticity may at least somehow be of relevance here.

The genus *Calciarcus* was described by Manton *et al.* (1977) as a side project to their work on circumscribing the new genus *Wigwamma*. The type material of *C. alaskensis* Manton *et al.* 1977 comprises a single cell (without flagella and haptonema) from Homer, S. Alaska. The *Calciarcus* coccolith superstructure is reminiscent of that of the type species of *Wigwamma*, *W. arctic*a Manton *et al.* 1977, in comprising a number of calcified struts that unite above the subtending organic base plate forming a tent-like superstructure. In this paper we account for the morphological diversity in *Calciarcus* spp. from both polar regions.

## MATERIALS AND METHODS

For the purpose of this paper we have with regard to the Southern Ocean considered material sampled from south of the Antarctic Convergence and in the northern hemisphere the Arctic Ocean and its surrounding ice-covered seas.

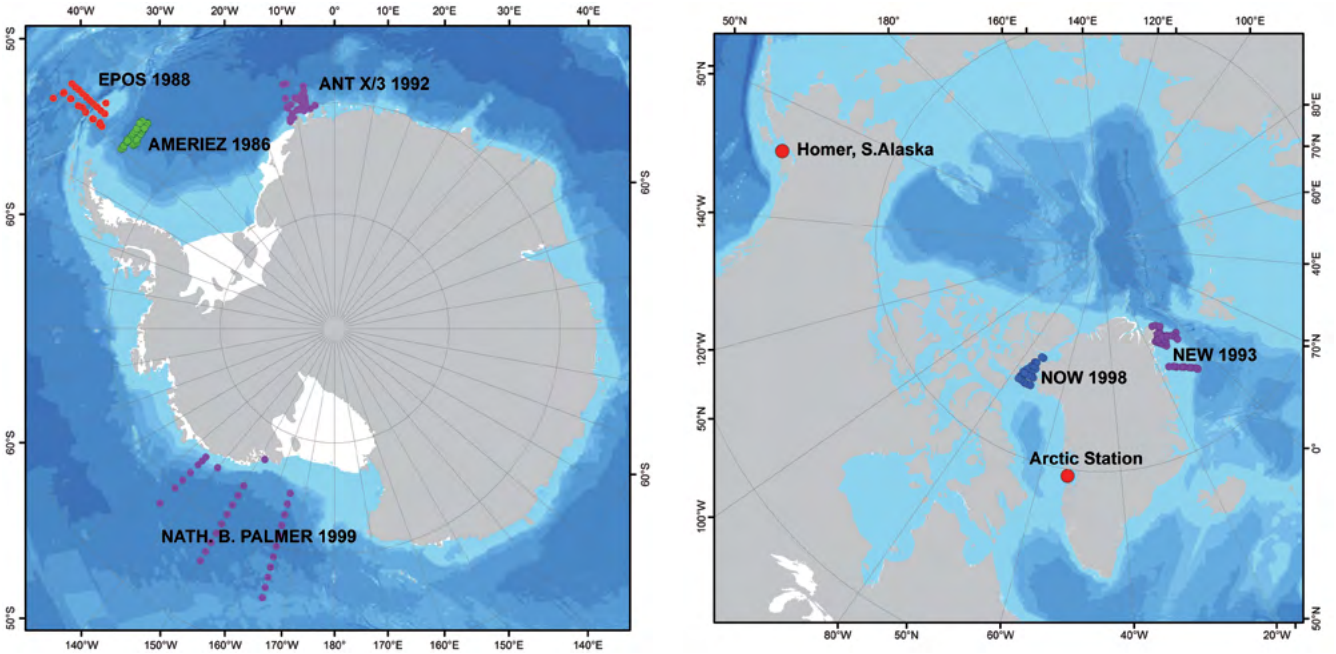
The Antarctic material originates from the R/V 'Melville' AMERIEZ cruise (March 1986), the R/V 'Polarstern' ANT VII/3 'EPOS II' cruise (Nov. 1988 – Jan. 1989) and the R/V 'Polarstern' ANT X/3 'Herbst im Eis' cruise (April–May 1992), with all cruises occupying stations in the Weddell Sea region (Fig. 1). Additional sampling took place in the Ross Sea on board the R/V Nathaniel B Palmer (Jan.–Feb. 1999 / NBP 99-01 Ice Cruise).

The Arctic material originates from the R/V 'Polarstern' ARK IX/3 North-East Water Polynya (NEW) cruise June–July 1993 and the R/V 'Pierre Radisson' North Water Polynya cruise (NOW) April–May 1998 (Fig. 2). Additional northern hemisphere sampling took place at the University of Copenhagen Arctic Station (Disko Bay, West Greenland) during the summers of 1988, 1990 and 1994 (Fig. 2).

The protocol for processing water samples for transmission electron microscopy and light microscopy were similar on all sampling occasions (see Thomsen *et al.* 2013 for further details).

## RESULTS

Micrographs and descriptions of *C. alaskensis* Manton *et al.* 1977 have been published on three occasions by Manton *et al.* 1977 (l.c. Figs 22–26), Thomsen 1981 (l.c. Figs 16–18) and Thomsen *et al.* 1988 (as *C. alaskensis* aff., l.c. Figs 21–22). Table 1 summarizes crucial morphological features extracted from published findings of *Calciarcus* spp. and adds additional information based on material from West Greenland (Disko), the high arctic (NEW) and Antarctica (EPOS, NBP).




**Figs 1–2.** Collection sites. **1** – map of the Antarctic region indicating sampling sites; **2** – map of the Arctic showing the location of sampling sites.

Apart from the factual information on the South Alaskan type specimen extracted for Table 1, the only other issue to touch upon here is the description of the calcified superstructure. Manton *et al.* (1977) refers to this as 'worm-like objects in a more or less cruciform arrangement lying on the outer face'. It is obvious from the illustrations accompanying the type description that the coccoliths display clear signs of decalcification as evidenced by the fact that the individual crystallites are difficult to distinguish. It is therefore in retrospect tempting to hypothesize that the worm-like appearance is in fact an artifact caused by advanced decalcification of the structures rather than being a genuine feature of this taxon. However, there is no doubt that Manton *et al.* (1977) are correct in the interpretation of the three-dimensional appearance of the coccolith where the length of the individual strut dictates that the superstructure can only be slightly arched above the base plate. Manton *et al.* (1977) unequivocally state that the superstructure has four support struts. While this is admittedly evident from one particular coccolith (Manton *et al.* 1977, l.c. Fig. 23, top of figure) it is otherwise difficult to ascertain whether this is a general feature of the type material.

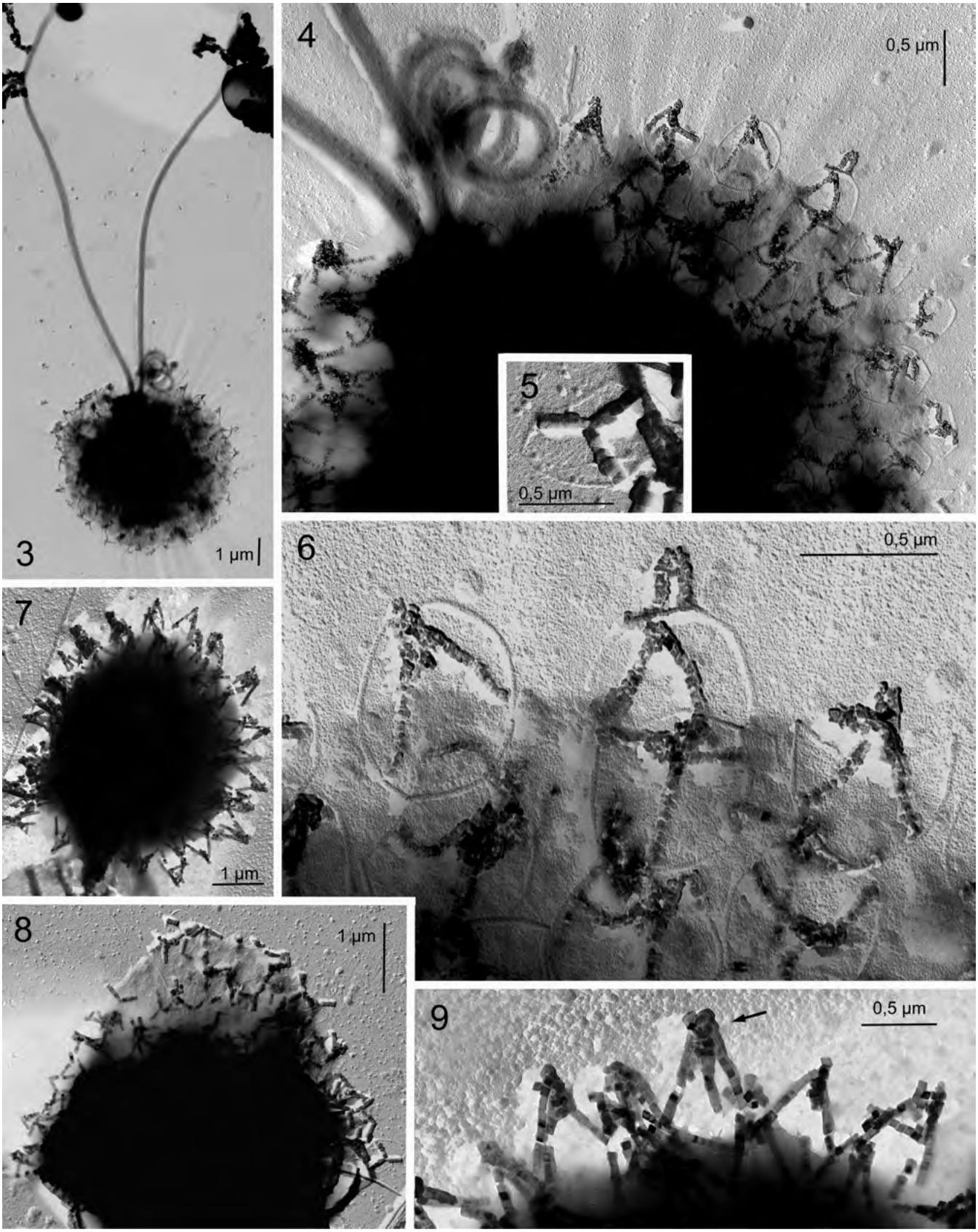
A single coccolithophorid specimen tentatively identified as *C. alaskensis* was reported from West Greenland by Thomsen (1981). The main differences between the West Greenland material (reproduced here as Figs 5, 8) and the South Alaskan type material concern the number of struts forming part of the calcified superstructure (3 versus 4) and the lack of a blunt spine terminating the superstructure in the West Greenland material.

Additional sampling in West Greenland (Østergaard 1993) revealed more material of *Calciarcus*. The complete cell (Figs 3, 4, 6) is much reminiscent of the *C. alaskensis* type material, yet deviating with regard to the number of struts forming part of the superstructure (3 versus 4) and also with respect to the fact that the superstructure arches somewhat higher above the organic base plate (c. 0.4 µm versus c. 0.2 µm). The West Greenland material (Figs 4, 6) shares with the South Alaskan type material a certain decalcification of the crystallites lined up to form the struts of the superstructure, which most likely contributes to impose on the individual strut a 'worm-like' appearance also in this material. A second cell from West Greenland (Figs 7, 9), referred to as *C. alaskensis* aff. in Østergaard (1993), displays fairly

**Table 1.** Morphological features and dimensions (µm) of *Calciarcus* morphotypes from all geographical sites.

| Reference | | Geographic origin | Morphotype 1 | Morphotype 2 | Morphotype 3 | Illustrations (this paper) | Protoplast | Flagella | Haptonema | Large scales | | Underlayer scales | | Superstructure | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Dimensions | Length | Length | Diameter | Shape | Size | Shape | Number of struts | Length of strut | Width of strut | Crystallites number | Termination | Height above scale centre |
| Manton *et al.* 1977 | Arctic | Homer, S. Alaska | | | | | | | | 0.6 | circular | 0.35 × 0.25 | oval | 4 | 0.35 | 0.05 | | blunt spine | 0.2 |
| Thomsen 1981 | | Disko, W. Greenland | | | | Figs 5, 8 | | | | 0.5 | circular | | oval | 3 | 0.3 | 0.04 | 5–8 | no spine | 0.15 |
| Østergaard 1993 | | Disko, W. Greenland | | | | Figs 3, 4, 6 | c. 5 | c. 15 | curled up | 0.6 | circular | | | 3 | 0.5 | 0.04 | 8–10 | blunt spine | 0.4 |
| Østergaard 1993 | | Disko, W. Greenland | | | | Figs 7, 9 | c. 4 | | | | | | | 3 | | 0.05 | > 10 | blunt spine | 1 |
| This paper | | NE Greenland (NEW) | | | | Figs 10–14 | c. 4 | 14–16 | 9 | 0.5 | circular | 0.3 | oval | 3-4 | 0.5 | 0.05 | > 10 | blunt spine | 0.5 |
| Thomsen *et al.* 1988 | Antarctic | Weddell Sea, Antarctica (AMERIEZ) | | | | Figs 18–20 | | | | | | | | 3 | | | > 10 | blunt spine | c. 1 |
| This paper | | Weddell Sea, Antarctica (EPOS) | | | | Figs 15–17, 21–26 | 3.5 | 13–14 | 12 | 0.7 | circular | | | 3 | 0.9 | 0.08 | > 10 | blunt spine | 1.25 |
| Gammelgaard 2000 | | Ross Sea, NBP | | | | Figs 27–28 | | | | | | | | 3 | | 0.05 | > 10 | blunt spine | > 1 |

**Figs 3–9.** *Calciarcus alaskensis* aff. TEM whole mounts from West Greenland (Arctic Station, Univ. Cph.). **3** – complete cell showing flagella and haptonema; **4** – anterior cell end of the organism shown in Fig. 3; **5** – high magnification of a single coccolith from the cell shown in Fig. 8. Notice that the struts of the superstructure are only slightly longer than the radius of the base plate; **6** – detail of coccoliths (same cell as depicted in Figs 3, 4) showing the unmineralized rimmed base plate and the 3-strutted pyramidal superstructure. The individual crystallite is partly dissolved; **7** – periplast comprising fairly robust coccoliths in which the superstructure arches high above the base plate centre; **8** – low magnification of partly complete cell. A single coccolith from the periplast is shown at higher magnification in Fig. 5; **9** – detail of coccoliths from the periplast shown at low magnification in Fig. 7. The crystallites are well preserved. Notice (arrow) that each superstructure terminates in a blunt spine (an irregular cluster of crystallites).



robust coccoliths with 3-strutted superstructures that arch high (c. 1 μm) above the scale centre (Fig. 7). The superstructure is terminated by a blunt spine formed by densely aggregated microcrystals (Fig. 9, arrow).

The NEW material from NE Greenland (Figs 10–14) proved to be fairly rich with regard to specimens that could tentatively be identified as *C. alaskensis* aff. The superstructures appear in this material as distinct conical structures that arch high above the base plate centre. The number of struts forming part of the structure seems in most cases to be three although in one particular case (Fig. 13, right hand coccolith) there are certainly four struts. The organic base-plate is flexible and in many cases irregularly folded (Fig. 13). The radial surface patterning is arranged in distinct quadrants (Fig. 11). There is no sign of any structural component that assists in attaching the individual strut to the marginal band of the unmineralized base-plate (Fig. 13). Despite the availability of cells it has proved difficult to verify the presence of unmineralized underlayer scales. However, it appears plausible to identify the minute organic scales pointed out in Fig. 10 as representing underlayer scales. These are similar in size and shape to those found in the South Alaskan type material.

Thomsen *et al.* (1988) for the first time recorded *C. alaskensis* aff. from the southern hemisphere. Details of the AMERIEZ material comprising just a single cell are reproduced here in Figs 18–20. The coccolith base plates are not visible due to the compactness of the periplast (Fig. 18). However, it is evident that the three-strutted superstructures arch high above the coccolith base plates. The crystallite substructure of the struts is particularly evident in this material (Figs 19, 20) as is also the blunt spine terminating a superstructure (Fig. 20, arrows).

The EPOS material from Antarctica (Figs 15–17, 21–26) comprised numerous cells that were tentatively identified as *C. alaskensis* aff. The three-strutted superstructures in this material arch high above the organic base plate and typically terminate in a short blunt spine (Fig. 21). The organic base plate is flexible and often folded (Fig. 21). There is no evidence of unmineralized underlayer scales. A certain size differentiation of coccoliths within a periplast, with slightly larger coccoliths clustering around the flagellar pole, is a characteristic feature of many cells (see e.g. Figs 15, 24). The frequent appearance of this species at certain sampling sites also rendered possible the identification of this taxon from light microscopy (Figs 16–17). However, it should be emphasized that in cases where the LM work is not backed up by species lists confirmed from using a TEM or a SEM, it is not possible to convincingly identify *C. alaskensis* aff. using the LM alone.

A few somewhat battered cells of *C. alaskensis* aff. (Figs 27–28) were found in samples from the Ross Sea (Gammelgaard 2000). The three-strutted, narrow and pointed superstructures arch high above the base plate. The Ross material did not allow for an examination of either base plates or underlayer scales.

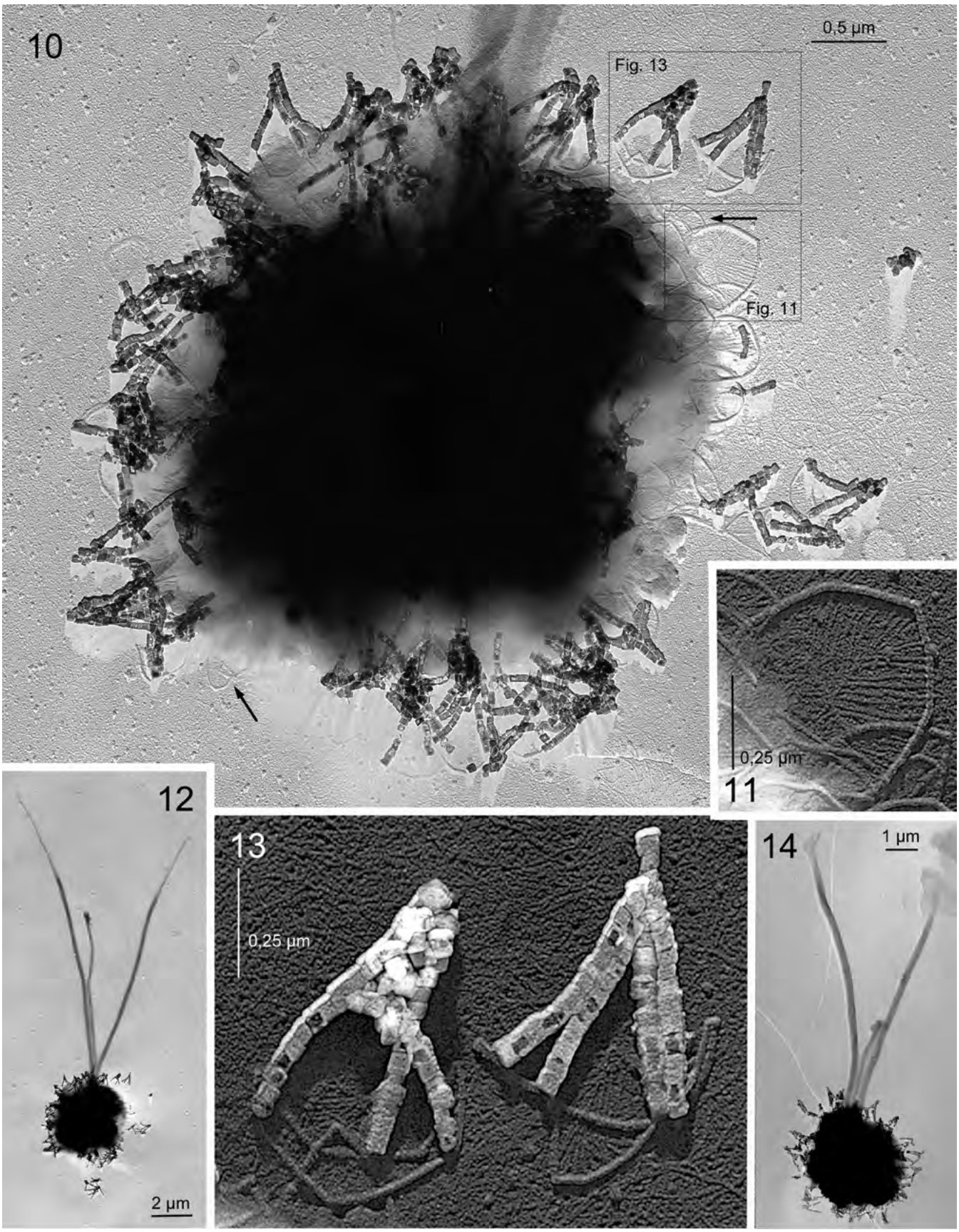
## DISCUSSION

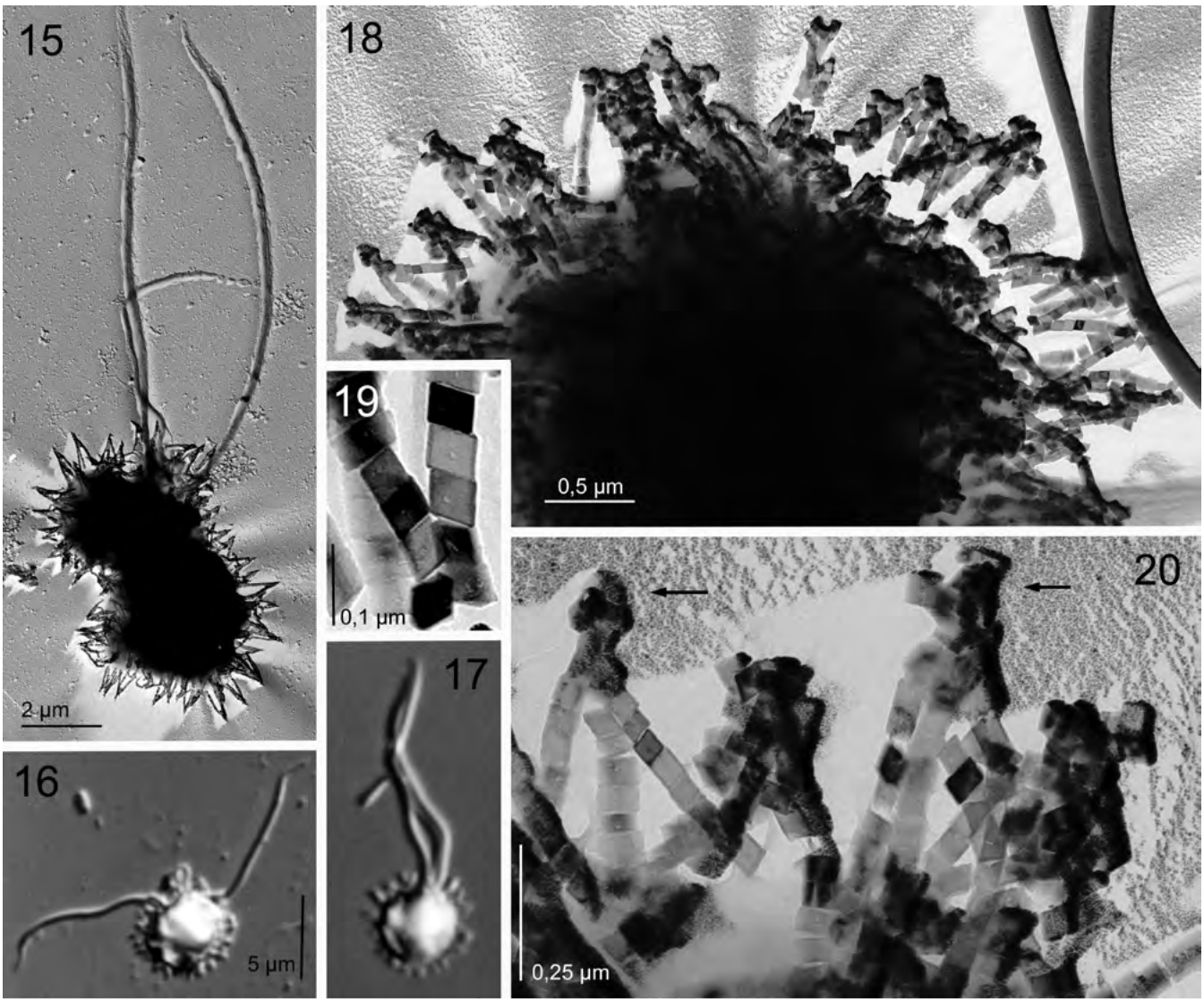
Based on the above survey of reported findings of organisms reminiscent of *C. alaskensis* and the tabulation of this information (Table 1) the next step will be first to evaluate whether the variability recorded can be accommodated within the generic description of *Calciarcus* as provided by Manton *et al.* (1977), and as second step to discuss if the variability recorded across the different collection sites calls for the description of additional taxa.

The generic diagnosis (Manton *et al.* 1977) reads as follows:

> *Coccolithophorid periplast with scales of two sizes, a lower layer of small oval unmineralized plates and an outer layer of larger circular unmineralized plates carrying a superstructure of four flexible calcified struts attached to the base of an abbreviated calcified spine. Both scale types with an unmineralized marginal band and a surface patterning of radiating ridges. Protoplast unknown.*

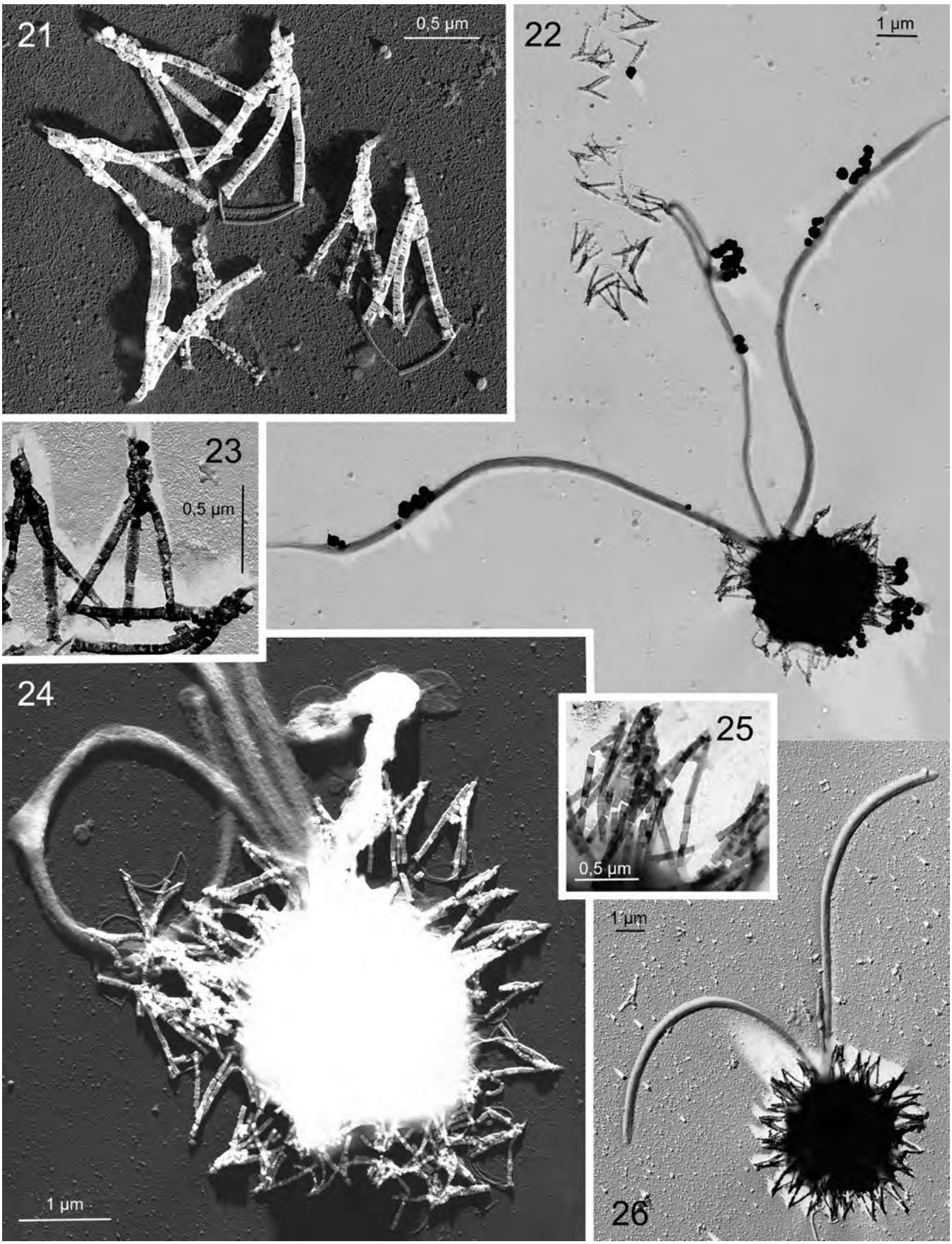
**Figs 10–14.** *Calciarcus alaskensis* aff. TEM whole mounts from the Arctic (NEW). **10** – detail of coccosphere from the cell shown in Fig. 12. Arrows point to presumed underlayer unmineralized scales; **11** – high magnification of organic base plate showing surface radiation in quadrants and a thickened margin of the scale. It is hypothesized that a calcified superstructure has been ripped away from this base plate during processing of the material; **12** – complete cell with flagella and haptonema; **13** – high magnification (reversed printing) of two detached coccoliths from the cell shown in Fig. 12. One coccolith superstructure (right) has 4 supporting struts, whereas the other appears to be furnished with only 3 struts; **14** – complete cell with flagella and haptonema.

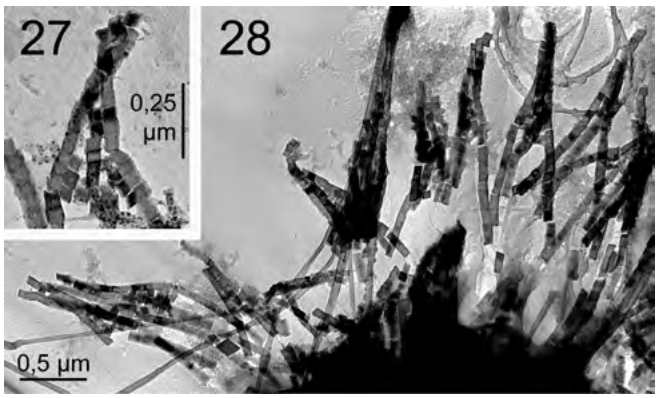





**Figs 15–20.** *Calciarcus alaskensis* aff. from Antarctica (Figs 15–17: EPOS; Figs 18–20: AMERIEZ); TEM (Figs 15, 18–20) and LM (Figs 16–17) whole mounts. **15** – pair of dividing cells; **16–17** – light micrographs (Nomarski optics) showing cells that are tentatively identified as *C. calciarcus*; **18** – whole cell collected during the AMERIEZ cruise lying next to a pair of choanoflagellate costal strips. Details from this coccosphere are shown at higher magnification in Figs 19, 20; **19** – high magnification of euhedral crystallites which piled on top of each other form part of a superstructure strut. The black crystallite towards the bottom of the picture is tilted and shows that one dimension of the rhombohedra is significantly shorter than the others; **20** – detail of a cluster of coccoliths in which the superstructure to the left clearly displays its three struts. All superstructures shown are terminated by a blunt spine (arrows) formed by a dense aggregation of crystallites.

**Figs 21–26.** *Calciarcus alaskensis* aff. TEM whole mounts from Antarctica (EPOS material). **21** – scatter of three-strutted coccoliths (detail from Fig. 22). Reversed printing; **22** – complete cell with flagella and haptonema and scatters of coccoliths that have become loose from the periplast; **23** – side view of a single coccolith showing a blunt spine (dense aggregate of crystallites) that terminates at the apex of the superstructure; **24** – part of a complete cell with flagella and haptonema. Notice that coccoliths clustering around the flagellar pole tend to be larger than those found elsewhere. Reversed printing; **25** – detail of coccolith superstructures that renders possible an estimation of the number of crystallites forming a single strut; **26** – complete cell with flagella and haptonema. Notice that in this cell the coccoliths appear to be of the same size throughout.






**Figs 27–28.** *Calciarcus alaskensis* aff. TEM whole mounts from Antarctica (Ross Sea). Micrographs courtesy of Marie Gammelgaard. **27** – detail of three-strutted superstructure; **28** – cluster of coccoliths. The superstructures are in this material particularly narrow and elongated.

The critical points to be addressed here is: 1) the reference to a superstructure consisting of four struts, 2) the flexibility of the individual strut, and 3) the presence of a calcified spine. While four struts is unequivocally documented from the type material and material from NEW (Fig. 13), it is also evident that the vast majority of coccoliths examined for the purpose of this investigation tend to be more appropriately described in terms of a three-strutted superstructure. However, it is surprising to realize how difficult it is to assess something as simple as the number of superstructure struts. Physical disturbance of the individual coccolith during preparation of the material for analysis in the TEM (drying, flattening), in combination with the fact that a superstructure strut can easily be concealed due to a partial or complete overlay of a neighbouring strut or a backwards bending of the blunt spine, are among the interpretational challenges. The critical question is whether variability in this feature is legitimate within a single specimen, a species or a genus. While the calcification in holococcolithophorid species is generally believed to be an external process (Rowson *et al.*1986) that is generally accepted to be physically constrained to a limited space sandwiched between the plasmalemma and an external skin coating, the organic base plate and most likely also an organic superstructure template of some kind are manufactured in the cell interior and extruded prior to calcification. The intracellular production of organic scales (in e.g. species of *Chrysochromulina*) or heterococcoliths (in e.g. species of *Wigwamma*) is generally characterized by a very high precision in terms of reproducing numerical and geometric features of the object. Coccoliths of e.g. *Wigwamma arctica* with any other number than four converging struts are as an example never found. As a starting point and based on the well supported conclusion that calcification is biologically controlled it appears valid to presuppose morphological and numerical stability also when it comes to holococcoliths. However, it is unknown to which extent e.g. the external envelope that assists in creating the right chemical environment for external calcification to occur, might also have some kind of molding effect during crystallolithogenesis that could impact on e.g. the final shape of a superstructure. Whereas it is fairly straightforward to establish as a rule that variability in the number of struts within the same type of coccolith should not be generally accepted in the case of species delineation, it is at the same time fairly obvious and supported by e.g. a reference to other genera that a numerical difference in the number of superstructure struts among species need not to be reflected at the generic level. In our opinion a species such as *Wigwamma triradiata* Thomsen in Thomsen *et al.* 1988 is thus well accounted for within the context of the genus *Wigwamma*, despite the fact that *W. triradiata* body coccoliths have a three-fold symmetry, while the type species, *W. arctica*, displays a four-fold symmetry (Thomsen *et al.* 2014).

As previously discussed we are inclined to explain the 'worm-like' and flexible appearance of a superstructure strut as at least partly an artifact caused by decalcification of the structure.

Finally we need to address the statement that a *Calciarcus* coccolith superstructure comprises struts that attach to an 'abbreviated calcified spine'. Among the illustrations selected for this publication there are a number of examples of coccolith superstructures that terminate in a calcified spine-like structure (see e.g. Figs 9, 20, 21, 23). A 'calcified spine' is in our material when best developed synonymous with an irregular aggregation of crystallites that represent a coalescence of the superstructure struts shortly before their distal termination. A similar interpretation seems to apply to the type material (Manton *et al.* 1977). It is also obvious when scrutinizing the material illustrated here, that a calcified spine is a feature that is often missing from numerous coccoliths, most likely due to mechanical distortion of the coccolith tips during handling of the cells and/or effects of decalcification. However, a calcified tip does

not appear to be a feature in the material examined by Thomsen (1981) and reproduced here as Figs 5, 8.

It is obvious from the above that although our understanding of the morphological variability within *Calciarcus* is still limited, it will nevertheless be appropriate based on the examination of a vastly increased number of cells to emend the genus diagnosis:

*Calciarcus* Manton, Sutherland & Oates 1977, p. 155 emend. Thomsen & Østergaard

> *Coccolithophorid periplast with scales of two sizes, a lower layer of small oval unmineralized plates and an outer layer of larger circular unmineralized plates carrying a superstructure of three-four sometimes flexible calcified struts often attached to the base of an abbreviated calcified spine which is typically formed by a coalescence of the calcified struts shortly before their distal termination. Both scale types with an unmineralized marginal band and a surface patterning of radiating ridges. Protoplast with two flagella and a somewhat shorter coiling haptonema.*

Despite the above analysis of fairly well preserved material of *Calciarcus* from a range of geographic sites, and the obvious morphological variability accounted for, it is still not evident how to deal with this variability in terms of perhaps distinguishing multiple taxa of *Calciarcus*. The number of calcified struts forming part of the coccolith superstructure and the elevation of this structure above the organic base plate are, when scrutinizing Table 1, the most likely features for such separation at the species level. However, as commented on above, an assessment of the number of struts is not trivial and the validity of this feature as a taxonomic marker inconclusive, while it also appears that the elevation of the superstructure above the base plate is continuous and hence not an immediate candidate for a segregation of species.

When evaluating the morphological variability encountered in the material available to us we tentatively identify three morphological clusters (see Table 1), i.e. 1) the South Alaskan type material and material from West Greenland (Figs 3, 4, 6) characterized by 3–4 flexible struts, a blunt terminating spine and a small elevation above the base plate (0,2–0,4 µm), 2) material from West Greenland (Thomsen 1981 and Figs 5, 8) characterized by 3 struts, no terminating spine and a low elevation above the base plate (0,15 µm), and 3) material from West Greenland (Figs 7, 9), NEW (Figs 10–14), AMERIEZ (Thomsen *et al.* 1988 and Figs 18–20) EPOS (Figs 15–17, 21–26) and NBP (Figs 27–28) characterized by 3–4 struts, a robust conical appearance of the coccolith and an elevation above the organic base plate typically around 1µm (0.5–1.25 µm).

We are at this stage inclined to refrain from describing new species of *Calciarcus* awaiting the finding of additional material and the application of different tools, e.g. SEM and/or genetic sequencing that might help in better establishing the boundaries among species of *Calciarcus*. The morphological variability demonstrated in this paper in combination with the fact that circumstantial evidence indicates that species of *Wigwamma* (5) and species of *Calciarcus* form part of diploid-haploid life histories (Thomsen *et al.* 1991, 2013) suggests the likelihood of more species of *Calciarcus* being discovered in the future.

The known biogeographical ranges of species of *Wigwamma* and *Calciarcus* morphotypes are indicated in Table 2. Two species of *Wigwamma*, *W. arctica* and *W. annulifera* are characteristic elements of the northern high latitude coccolithophorid community, while a handful of *Wigwamma* species is consistently found to be present in samples processed from the southern high latitudes.

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**Table 2.** Biogeographical overview with reference to *Wigwamma* spp. and morphotypes of *Calciarcus alaskensis*.

| Region | Northern hemisphere | | | | | | | Southern hemisphere | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locality | W. Greenland (Disko) | North Water Polynya (NOW) | Resolute Bay, Cornwallis Island | North East Water Polynya (NEW) | Svalbard | Homer, S. Alaska | Denmark | Cape Town, S. Africa | Weddell Sea (AMERIEZ) | Weddell Sea (EPOS) | Weddell Sea (ANT X73) | Ross Sea (NBP 99-01) | Australian sector / Southern Ocean |
| ***Wigwamma*** | | | | | | | | | | | | | |
| *W. annulifera* | 4,7,8 | | | 5,1 | 5 | 1 | | 1 | 2 | 5 | 5 | | |
| *W. antarctica* | | | | | | | | | 2 | 5 | 5 | | 9 |
| *W. arctica* | 1,4,6,7,8 | 10 | 1 | 5,1 | | | 3 | | 2 | 5 | 5 | | |
| *W. armatura* | | | | | | | | | 5 | | 5 | | |
| *W. triradiata* | | | | | | | | | 2 | 5 | 5 | 10 | 9 |
| ***Calciarcus*** | | | | | | | | | | | | | |
| *C. alaskensis (mt 1)* | 8 | | | | | 1 | | | | | | | |
| *C. alaskensis (mt 2)* | 4 | | | | | | | | | | | | |
| *C. alaskensis (mt 3)* | 8 | | | 11 | | | | | 2 | 11 | | 10 | |

1) Manton *et al.* 1977
2) Thomsen *et al*. 1988
3) Thomsen, unpublished data
4) Thomsen 1981
5) Thomsen *et al*. 2013
6) Hansen *et al*. 1988
7) Clausen *et al*. 1994
8) Østergaard 1993
9) Findlay and Giradeau 2000
10) Gammelgaard 2000
11) This publication

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